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Different morphology of *Nuphar lutea* in two contrasting aquatic environments and its effect on ecosystem engineering

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Earth Surface Processes and Landforms

ABSTRACT: Aquatic plants (macrophytes) can have a large effect on river hydraulics and geomorphology. Though, the extent to how plant morphological plasticity actively influences these feedbacks has received little scientific attention. The nymphaeid macrophyte species *Nuphar lutea* (L.) Smith is characterized by a distinct leaf duality. Floating leaves shade most of the submerged leaves thereby limiting light penetration in the water. Despite their apparent negligible photosynthetic role, submerged leaves of *N. lutea* remain intact during summer and contribute a significant part to the total biomass. Our results indicate that the submerged leaves are crucial in plant–flow interactions and hence in the engineering potential of the plant, i.e. the capacity to locally reduce flow velocities and to promote sedimentation, including organic matter deposition. Plant individuals growing in running river water were compared to individuals from adjacent oxbow lake water. The number and size of submerged leaves were significantly higher for river standing individuals and the accumulated sediment contained significantly more organic matter, total nitrogen and total phosphorus, and was characterized by a lower carbon/nitrogen ratio and a finer grain size. We therefore argue that the submerged *N. lutea* canopy in rivers has the ability to create a high-nutrient, low hydrodynamic environment, resembling the conditions found in oxbow lakes. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: Biebrza; scale-dependent feedbacks; morphological plasticity; bio-geomorphology; aquatic vegetation; nutrient dynamics; organic matter accumulation

Introduction

Multiple studies have demonstrated that plants can significantly affect river channel form and adjustment (Tal and Paola, 2007; Hicks *et al.*, 2008; Larsen and Harvey, 2010, 2011; Montakhab *et al.*, 2012). There is a growing scientific interest in these plant–river interactions (e.g. Franklin *et al.*, 2008; Gurnell *et al.*, 2010; Zong and Nepf, 2010; Nepf, 2012), focusing mostly on riparian plant species, particularly shrubs and trees. However, true aquatic macrophytes can also affect the hydraulics and geomorphology of rivers (Gurnell *et al.*, 2010; Bertoldi *et al.*, 2013). Growing in patches, they can act as ecological engineers (Gurnell, 2014) meaning that they are capable of adapting the environment to their benefit, with positive and/or negative feedbacks. Flow velocity, for instance is reduced inside macrophyte patches, as friction is generated by the canopy (Vandenbruwaene *et al.*, 2011; Schoelynck *et al.*, 2012). Adjacent to patches, flow velocity is increased because of flow deviation around the patches (Schoelynck *et al.*, 2012). As a consequence, shoots inside patches have a better survival chance and a larger primary production than shoots emerging between patches, where erosion, scouring and uprooting can limit here plant growth and patch expansion (Schoelynck *et al.*, 2012). Macrophyte patches thus create spatial variability in stream velocity and induce geomorphological changes of the river including (i) changes in bathymetry (Cotton *et al.*, 2006; Schoelynck *et al.*, 2012; Schoelynck *et al.*, 2013) and (ii) bank erosion leading to meandering (Gurnell, 2014, and references cited therein).

Apart from river studies, knowledge of vegetation–hydrodynamics–geomorphology interaction is also rapidly emerging from studies in coastal and estuarine environments. Bouma *et al.* (2007); Temmerman *et al.* (2007); Van Wesenbeeck *et al.* (2008) and Vandenbruwaene *et al.* (2011), for instance, clearly showed differences in stream velocity in and around vegetation patches of the tidal marsh grass *Spartina anglica* C.

E.Hubb, causing increased sedimentation in the patches, and eroding gullies around the vegetation. Bouma *et al.* (2009) proposed a size-dependence of these plant–flow interactions, with clear threshold values as they state that a minimum patch size and minimum organism density within the patch is needed before habitat modification can occur. This means decreasing flow velocities within the vegetation (i.e. positive feedback) and increasing flow acceleration alongside the vegetation patch (i.e. negative feedback). The combination of positive feedbacks within and negative feedbacks outside the vegetation are generally referred to as scale-dependent feedbacks (Rietkerk and Van de Koppel, 2008). Such feedbacks were recently also demonstrated to result in spatial self-organization of riverine vegetation (Schoelynck *et al.*, 2012).

The extent to which plant morphological plasticity can actively influence these scale-dependent feedbacks has received little scientific attention. The nymphaeid macrophyte species *Nuphar lutea* (L.) Smith (Figure 1) is characterized by a distinct leaf duality. *Nuphar lutea* is common in the temperate regions of the northern hemisphere (Heslop-Harrison, 1955): it occurs both in lakes with little hydrodynamic stress as well as in flowing streams. They prefer depths between 0.6 m and 2.4 m (Heslop-Harrison, 1955). Translucent, crumpled submerged leaves are produced in early spring; leathery floating leaves emerge later and reach the water surface in April and May. The occurrence of submerged leaves during the whole growing season is less explicitly found among other nymphaeid species (Smits *et al.*, 1988), and the reason for this summer presence is unstudied. Shoot density and leaf orientation in vegetation are classically explained in relation to photosynthetic success (McMillen and McClendon, 1979; Binzer and Sand-Jensen, 2002). However, floating leaves covering most of the submerged leaves (Figure 2) are likely to limit light penetration in the water and the photosynthetic potential of the submerged leaves. Still, despite this hypothesized negligible photosynthetic role, submerged leaves of *N. lutea* remain intact during summer and contribute a significant part of the total biomass (Snir *et al.*, 2006). Flow velocities may evoke strong hydrodynamic forces on the (submerged) shoots and leaves, obliging the plant to invest in energy-expensive tissue reinforcement to withstand them (Schoelynck *et al.*, 2010): the presence of submerged leaves thus seems counterproductive. Other rooted, floating-leaved species like *Potamogeton natans* L. minimize their submerged biomass and concentrate all leaves at the water surface which maximizes their photosynthetic success and minimizes hydrodynamic forces (Bal *et al.*, 2011).

Figure 1. *Nuphar lutea* (L.) Smith individual from the Biebrza National Park (Poland). Picture was taken outside the water lying on a white background. Starting from a rhizome, six translucent, crumpled submerged leaves (1–6), three leathery floating leaves (a–c) and one flower bearing stem originate. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

We argue that the submerged leaves are crucial in plant–flow interactions (Bal *et al.*, 2011; Puijalon *et al.*, 2011) and hence in the engineering potential of the plant, i.e. the capacity to alter flow velocities and to promote sedimentation including organic matter deposition. Higher sediment organic matter content may lead to higher nutrient and carbon availability (Brock *et al.*, 1985; Webster and Benfield, 1986; Snir *et al.*, 2006), improving plant productivity within the patches. This is especially important for an eutraphent species like *Nuphar lutea* (Bornette and Puijalon, 2011).

By means of field measurements, we investigate two possible reasons for the presence of submerged leaves on *Nuphar lutea* individuals at periods of peak biomass. We hypothesize that:

Hypothesis 1 *Nuphar lutea* is an ecosystem engineer: the submerged leaves are efficient in reducing flow velocity thereby increasing organic matter deposition and hence nutrient availability. The efficiency of reducing the flow velocity depends on size and density of the patch: investing in submerged leaves is hence only valuable in running river water and not in still oxbow lake water, implying morphological

Figure 2. Picture of a *Nuphar lutea* patch in the river Sidra, near the village of Harasimowicze, which is location 1 in Figure 3. This patch is representative of all patches measured in the river in this study, though blockage factor (ratio patch width to river width) may vary among the different locations. Floating leaves cover most of the water surface and shade the submerged leaves to a great extent. To the right of the patch, ripples are visible on the water surface, probably resulting from flow acceleration adjacent to the patch and flow deceleration inside the patch. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

differences between plants growing under different hydrodynamic regimes.

Hypothesis 2 Floating leaves of *Nuphar lutea* prevent light from reaching its submerged leaves, making the latter redundant for photosynthesis and should therefore not be retained as an explanation for the existence of submerged leaves.

Materials and Methods

Study site

Nuphar lutea (L.) Smith is a common macrophyte in the Biebrza River, a tributary of the Narew River in north-eastern Poland. The river is approximately 160 km long, up to 80 m wide and has a catchment area of *c.* 7000 km^2. It runs through a sandy bed (median grain size D_{50} is 365 µm), it has an average annual discharge of *c.* 30 $m^3 s^{-1}$, and it has an average water-surface slope of 0.016% between Sztabin and Goniądz. The acidity of the river water is neutral to slightly alkaline (Wassen *et al.*, 2006), which is favorable for the occurance of *N. lutea* (Smits *et al.*, 1988). This species has a smaller ecological amplitude with respect to alkalinity in comparison to other nymphaeid species, and is also a typical eutraphent species which prefers a high nutrient availability (Bornette and Puijalon, 2011). This makes it abundant in typical nutrient rich lowland rivers. The floodplain is relatively undisturbed; the river has a natural channel pattern which is characterized by a single-thread meandering channel and small oxbow lakes. Due to the low agricultural fertilizer input the impact on nutrient cycles is low and a species rich flora still occurs in the Biebrza River and valley. Nutrient concentrations for 2008 in the upper catchment are: $(NO_2^- + NO_3^-)$-N = 0.18 ± 0.02 mg l^{-1}; NH_4^+-N 0.08 mg l^{-1}; PO_4^{3-}-P = 0.04 ± 0.02 mg l^{-1}. The macrophyte community in general can have a maximum biomass of 175 g DM m^{-2} in the upper basin, for *N. lutea* specific this is up to 200 g DM m^{-2} (personal observations in 2009). *Nuphar lutea* has an average stem and petiole density of 6 per m^2 ground surface and a total submerged leaf area of 0.22 m^2 per m^2 ground surface. Patches of *N. lutea* are generally a few meters long (2–10 m), but may extend up to 30+ m. The width of the patch is variable, and so is the blockage factor in the river (ratio patch width to river width). The patches we used in this study are estimated to fill about 50–60% of the river width in the upstream sites, to less than 10% in the most downstream site.

Five locations along the Biebrza River were selected on accessibility, presence of a nearby small oxbow lake and the presence of *Nuphar lutea* patches in the river and in the oxbow lake (Figure 3). The study was done in June of three consecutive years (2007–2009) which had similar hydraulic conditions (Table I) and similar vegetation conditions. For a more detailed description of the eco-hydrological functioning of the Biebrza River valley, see Wassen *et al.* (2006).

Vegetation sampling and biometric analysis

The five locations along the Biebrza River were sampled in June 2008. On each location, one river patch and one lake patch were selected. Five *Nuphar lutea* individuals were sampled in each of the selected river patches, and three in each of the selected lake patches. The entire plants were cut just above the roots. This resulted in total in 25 riverine individuals and 15 lake individuals. The number of flowers and buds, stems, floating leaves, submerged leaves, petioles of floating leaves and petioles of submerged leaves of each individual

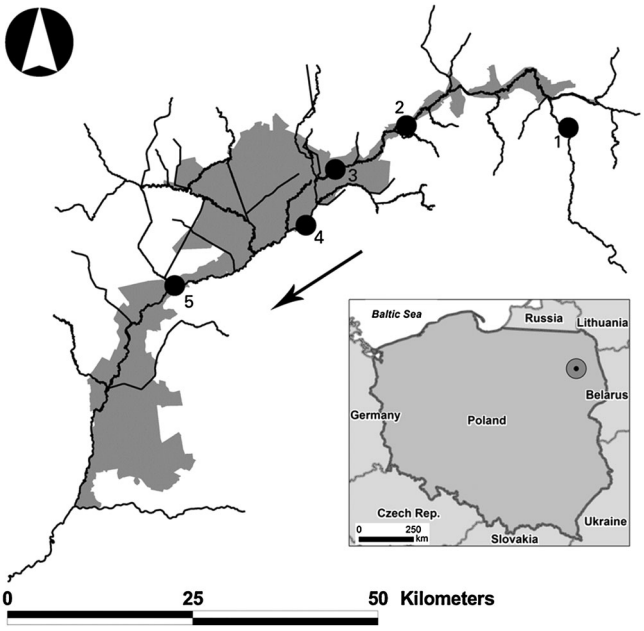

Figure 3. Map of the Biebrza River in the Biebrza National Park, with park borders indicated in gray. The arrow indicates the main water flow direction. The park is located in the north-eastern part of Poland. A country map is inserted with the exact location of the National Park indicated with a ⊙ symbol (park headquarters at N53.449001, E22.626008). Vegetation and sediment samples were taken at different sites along the river and in adjacent oxbow lakes, located less than a few 100 m from the main channel. Sample locations, from upper towards middle basin, were situated nearby the following villages: Harasimowicze (on Sidra, tributary of Biebrza (1)), Sztabin (2), Jagłowo (3), Dolistowo Stare (4) and Goniądz (5). Velocity and light climate were measured on profiles through a *Nuphar lutea* patch in the Sidra River, near the village of Harasimowicze (1).

were counted. Petioles are elliptically shaped (eye-shaped), and so the diameter of both the major and minor axes of the petiole was measured. Stems are circular and one diameter measurement sufficed. Diameters were determined using a digital caliper measuring width (in millimeters) on 0, 25, 50, 75 and 100% of the length and averaged afterwards per petiole or stem. All floating and submerged leaves were spread out and photographed on a grid to determine the leaf area (LA; in m^2) by digital image processing. The following characteristics were calculated per leaf type for each plant individual both from river and lake sampling locations:

(i) Mean leaf area (LA_{mean}; in m^2): average LA per leaf type (floating or submerged) and per habitat (lake or river).
(ii) Mean total leaf area (LA_{total}; in m^2): average total LA of an individual per leaf type and per habitat.
(iii) Mean total specific leaf area (SLA_{total}; m^2 kg^{-1}): average total SLA of an individual per leaf type and per habitat, with SLA = LA per unit leaf dry matter (Cornelissen *et al.*, 2003).

Sediment sampling and chemical analysis

In each of the selected patches (before the vegetation sampling), as well as in non-vegetated zones adjacent to the patches, five sediment cores (∅: 0.06 m, depth: 0.20 m of which the top 0.03 m was used) were taken with a sediment corer (Beeker, Eijkelkamp, Giesbeek, The Netherlands). Sediment cores adjacent to the patch were taken in zones with no vegetation at all (also no other species), yet as close as possible to the original patch (cross-stream, usually a few

Table I. Basic hydraulic data of three years (June) of the Biebrza River on five locations relevant for this study

		2007	2008	2009
Sidra Distance from Belarus border = 29 km	River width (m)	7.5	n.a.	n.a.
	Maximum river depth (m)	0.9	n.a.	n.a.
	Discharge ($m^3 s^{-1}$)	(0.24)[a]	n.a.	n.a.
Sztabin Distance from Belarus border = 71 km	River width (m)	19.7	22.0	17.8
	Maximum river depth (m)	2.1	2.1	2.1
	Discharge ($m^3 s^{-1}$)	0.97	0.86	1.06
Jagłowo Distance from Belarus border = 91 km	River width (m)	16.3	12.0	12.2
	Maximum river depth (m)	1.5	1.4	1.4
	Discharge ($m^3 s^{-1}$)	1.08	1.14	1.44
Dolistowo stare Distance from Belarus border = 104 km	River width (m)	25.9	23.0	29.4
	Maximum river depth (m)	2.6	2.1	2.1
	Discharge ($m^3 s^{-1}$)	5.28	3.30	6.62
Goniądz Distance from Belarus border = 122 km	River width (m)	44.8	57.7	60.3
	Maximum river depth (m)	2.5	3.0	3.4
	Discharge ($m^3 s^{-1}$)	6.24	5.01	7.08

Note: Discharge is measured using a tape measure for river width and depth, and a propeller (OTT C31-87200) to measure the stream velocity; distances to the Belarus border are calculated in GIS; n.a., not available.
[a]Actual discharge was not measured in 2007 at Sidra. The value given is an indicative value from 2000, when hydraulic conditions were comparable to the 2007 situation.

meters apart). Samples were dried for 48 hours at 70 °C and sieved afterwards over a 1 mm mesh to remove larger particles and to obtain homogeneous samples (gravel removal from the mineral fraction and wood from the organic fraction). Total nitrogen and total phosphorus content were determined according to Walinga *et al.* (1989): samples were digested with sulfuric acid (H_2SO_4), salicylic acid and hydrogen peroxide (H_2O_2) and subsequently analyzed on a colorimetric segmented flow analyzer (SAN^{++}, Skalar, Breda, The Netherlands). The organic matter content was determined by loss on ignition (Heiri *et al.*, 2001). Samples were heated to 105 °C for two hours and weighed. Thereafter, samples were ignited at 550 °C for four hours and weighed again. The difference between both gives an index of the organic matter present in the sample. Dividing organic matter by 1.8 gives the amount of carbon present (in mg g^{-1}) (Schlesinger, 1977; DIN38414/S3, 1985). Carbon/nitrogen (C/N) ratios are a good predictor of the rate of organic matter decomposition (Taylor *et al.*, 1989). Grain size distribution was determined using a laser diffraction unit (Mastersizer S, Malvern Instruments, Worcestershire, UK) and classified following the Udden (1914) and Wentworth (1922) scale.

Flow and light measurements

In June 2009, at the middle of the patch width, stream velocities were measured 0.3 m upstream and 0.3 m downstream of the submerged canopy of eight *Nuphar lutea* patches with a different submerged canopy length (ranging between 1 and 7 m). The five locations where this was done were equal to the 2008 sampling campaign sites (Figure 3), but the patches were not necessarily the same, because we chose to focus on patches with a broad variety in length rather than to be able to directly compare the data from both years. Stream velocity was measured on one-third and two-thirds of the submerged canopy height (measured from the stream bed) using an electromagnetic flow meter (EMF; Valeport model 801, Totnes, UK) over a sampling period of 60 seconds at a sampling rate of 1 Hz and averaged afterwards. A reduction efficiency was calculated as the difference between the stream velocity upstream and downstream the patch at the same depth, divided by the respective upstream velocity. This way we were able to relate the blocking effect of a patch in a relative way to the submerged canopy length which was measured with a tape measure. Detailed flow and light conditions were measured in June 2007 on profiles through a *N. lutea* patch in the Sidra River, a channelized tributary to the Biebrza River near the village of Harasimowicze (Figure 3). The selected patch was 7 m long, 2.5 m wide and growing in a stretch with an average width of 7.5 m and a maximal depth of 0.9 m. This patch was also measured in the 2008 and 2009 campaigns. Measurements were made on four profiles of which three were inside the patch and one was at a non-vegetated location 3 m upstream of the patch. Inside the patch, one profile was measured at the upstream part of the patch where the flow velocity had pushed the floating biomass further downstream and hence only submerged biomass occurred. The other two profiles, one in the middle and one at the downstream end of the patch, went through a well-developed floating and submerged canopy. Profile depth interval was 0.1 m from the water surface until −0.7 m, and with an extra measurement at −0.05 m. The total water depth was also recorded. Stream velocity was measured using an EMF (Nautilus C 2000, Ott Hydromet, Kempten, Germany) over a sampling period of 60 seconds at a sampling rate of 1 Hz and averaged afterwards. Light conditions were measured using an underwater LI-COR quantum sensor (LI-185B, LI-COR Biosciences, Lincoln, NE, USA) at the same locations as the stream velocity measurements. The underwater quantum sensor measures quantum radiation in μmol $m^{-2} s^{-1}$ (=6.02×10^{17} photons $m^{-2} s^{-1}$). The sensor is used for measuring PAR (photosynthetically active radiation) in aquatic environments and has a 400–700 nm quantum response. Both the immersion effect and the cosine effect are accounted for by the potentiometer connected to the sensor.

Statistics

Statistical tests were performed in SAS 9.1 (SAS Institute Inc., Cary, NC, USA). One-way analysis of variance (ANOVA) followed by a *post hoc* Tukey HSD (honest significant difference) correction was conducted to test mean differences in parameters between lake and river sediment samples and lake and river standing *Nuphar lutea* individuals. A principal component analysis (PCA) ANOVA was used to classify grain size. A Spearman rank correlation test was applied to test for relations between variables.

Results

Biometric data are summarized in Table II. The number of submerged leaves and associated petioles was significantly higher for river standing individuals than for lake standing individuals ($p < 0.001$). River submerged individuals had a mean leaf area and mean total leaf area that were significantly higher than those in lakes ($p < 0.001$). This means that the river standing individuals have more and larger submerged leaves, resulting in more leaf area that can be in interaction with the flow. No difference of these parameters was found for floating leaves. For both leaf types, no difference in mean total specific leaf area was observed between river and lakes. Grouping both habitats, the mean total specific leaf area of submerged leaves was up to 2.7 times larger than that of floating leaves. All other biometric data (Table II) did not show significant differences between both habitats except for stem length (+22% in river) and submerged petiole length (+27% in river).

Sediment taken within *Nuphar lutea* patches in the river contained significantly more organic matter, and more total nitrogen and total phosphorus than sediment from non-vegetated locations in the river (Figures 4a–4c; $p < 0.05$). For lake samples, no significant differences in sediment organic matter, total nitrogen and total phosphorus concentrations were observed between samples from the *N. lutea* stands and the non-vegetated locations. A comparison of the C/N ratio in all four groups of sediment samples (Figure 4d) shows that only the C/N ratio in the sediment of non-vegetated river locations was significantly higher ($p < 0.05$). Non-vegetated river samples had little very fine sand (63–125 µm) and fine sand (125–250 µm) but more coarse sand (500–1000 µm) compared to other samples ($p < 0.0001$). This results in a larger D_{50} grain size in non-vegetated river samples (calculated as the mean of the D_{50} values of all replicate samples), differing significantly from vegetated river samples and vegetated and non-vegetated lake samples (Figure 4e).

Stream velocity in the river at the non-vegetated location upstream of the patch near Harasimowicze declines with depth (Figure 5a). Profiles inside the patch are modified with lower velocities at the top 0.1 m layer if floating leaves are present (profiles (iii) and (iv)), higher velocities below the floating leaves and above the submerged leaves (all profiles) and strongly reduced velocities inside the submerged leaves (all profiles). This reduction generally causes lower flow velocities downstream of the patch, relative to the upstream flow velocity on both investigated depths (Figure 6). Reduction efficiency is positively related to patch length ($R^2 = 0.70$; $p < 0.001$) with longer patches generally causing a more efficient reduction in velocity, sometimes up to 100%, which means the water is stagnant at the distal end of the patch.

Light intensity declines with depth at the non-vegetated location upstream of the patch (Figure 5b). The same was measured in profile (ii) above the submerged biomass, but as soon as the profile entered the biomass, light intensity declined drastically. Profiles (iii) and (iv), both shaded by a floating biomass, show a light intensity of nearly 0 µmol m^{-2} s^{-1} at all depths.

Discussion

Nuphar lutea individuals growing in running river water had significantly more submerged leaves with a larger total leaf area than individuals standing in the adjacent oxbow lakes. In running river water, the large submerged leaves of *N. lutea* reduced the flow velocity. This likely caused the increased amount of smaller sediment particles and organic matter found in the sediments within *N. lutea* patches relative to non-vegetated parts of the river bed, analogous to other studies on submerged macrophytes (Sand-Jensen, 1998; Cotton *et al.*, 2006; Kleeberg *et al.*, 2010). Organic matter concentration in the sediment of the riverine *N. lutea* patches was up to six times higher than the concentration found in non-vegetated zones of the river.

Table II. Biometric data of lake and river standing *Nuphar lutea* individuals

		Location lake		Location river		
		Mean	SD	Mean	SD	*p*-Value
Flowers	#	1.7	0.9	1.7	0.9	
Stems	#	1.6	0.8	1.7	0.6	
	l	0.63	0.17	0.77	0.26	< 0.01
	$\varnothing_{a=b}$	0.0079	0.0013	0.0080	0.0011	
Petioles of	#	4.6	2.3	7.3	3.2	< 0.01
submerged leaves	*l*	0.49	0.21	0.62	0.27	< 0.001
	$\varnothing_a$	0.0055	0.0012	0.0058	0.0010	
	$\varnothing_b$	0.0085	0.0018	0.0087	0.0013	
Petioles of	#	5.5	2.3	4.0	2.1	
floating leaves	*l*	0.67	0.31	0.73	0.30	
	$\varnothing_a$	0.0066	0.0015	0.0065	0.0011	
	$\varnothing_b$	0.0095	0.0020	0.0094	0.0014	
Submerged leaves	#	4.6	2.3	8.4	3.3	< 0.001
	LA_{mean}	0.0347	0.0260	0.0527	0.0331	< 0.001
	LA_{total}	0.15	0.06	0.44	0.04	< 0.001
	SLA_{total}	37.9	8.7	37.7	6.3	
Floating leaves	#	5.5	2.3	4.8	2.5	
	LA_{mean}	0.0299	0.0181	0.0330	0.0148	
	LA_{total}	0.17	0.04	0.15	0.02	
	SLA_{total}	11.7	2.7	15.1	4.0	

Note: Data are averages of 25 river individuals and 15 lake individuals, over five different locations along the downstream gradient of the river with standard deviation (SD). # = number per individual, *l* length (in meters), $\varnothing_a$ = smallest diameter (in meters), $\varnothing_b$ = largest diameter (in meters) perpendicular on $\varnothing_a$, LA_{mean} = mean leaf area (in m^2), LA_{total} = mean total leaf area (m^2), SLA_{total} = mean total specific leaf area (in m^2 kg^{-1}). Significant differences are calculated with a two-way ANOVA, followed by post-hoc Tukey's HSD correction.

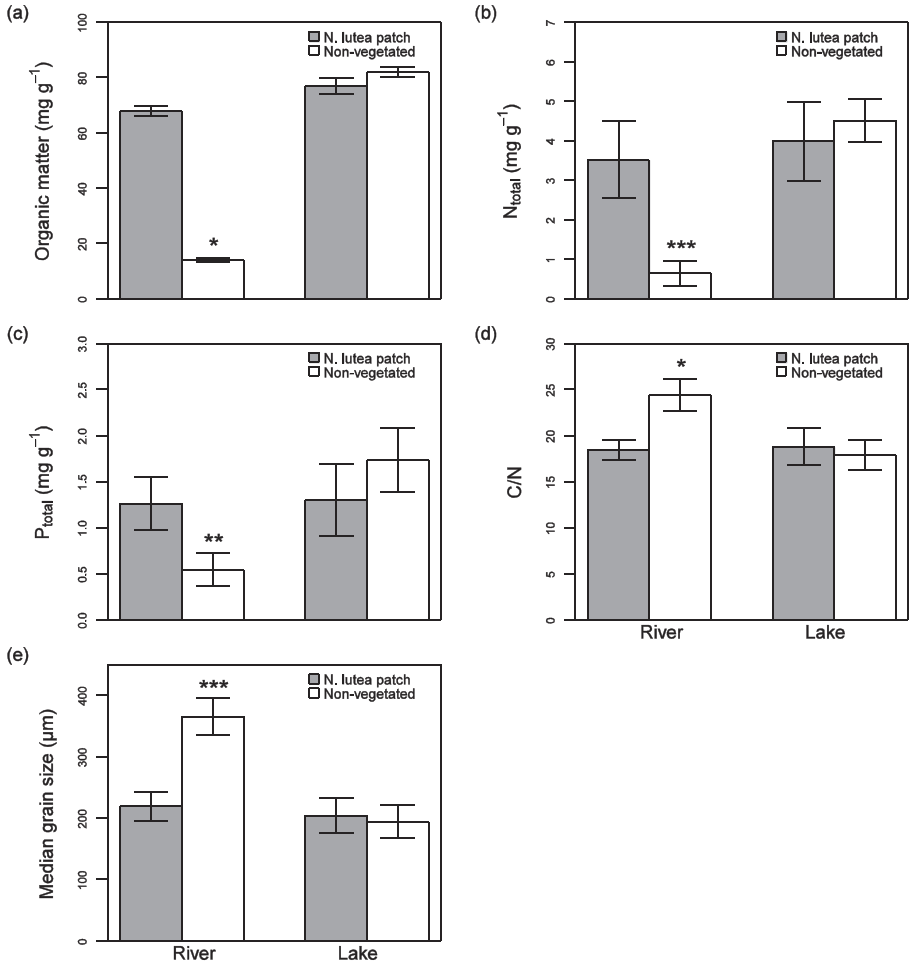

Figure 4. (a) Mean organic matter content (mg g^{-1} ± standard error [SE]), (b) total nitrogen content (mg g^{-1} ± SE) of the entire sample, (c) total phosphorus content (mg g^{-1} ± SE) of the entire sample, (d) C/N ratio of the organic matter (±SE) and (e) mean D_{50} grain size (µm ± SE) of sediment samples (<1 mm) taken from *Nuphar lutea* patches and from non-vegetated locations compared between lake and river. Significant differences are calculated with a one-way ANOVA, followed by post-hoc Tukey's HSD correction and preceded by a $\log_{10}$ transformation in panel (a); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Sample size (n) = 25 in the river and 15 in the lakes.

Furthermore, the combination of a higher particulate nutrient stock (total nitrogen and total phosphorus) and a lower C/N ratio of the organic matter within riverine *N. lutea* patches indicates that the organic matter in the patches has the potential to break down rapidly into a large dissolved nutrient stock (Soetaert *et al.*, 1996), so that nutrient availability can be higher within riverine *N. lutea* patches as compared to the non-vegetated river parts. This could be an advantage for the eutraphent *N. lutea* in the mesotrophic Biebrza River. Having a larger total submerged leaf area can therefore be considered as a benefit in the river and can fulfil the criteria required to be termed an ecosystem engineer (Jones *et al.*, 1997). The engineering capacity is also size-dependent as the efficiency of the patch to reduce the flow was positively related to patch length.

In contrast, in the oxbow lakes, organic matter concentrations, particulate nutrient stocks and C/N ratios were equal inside and outside *Nuphar lutea* patches, and equal to the values found inside river standing *N. lutea* patches. This indicates that organic matter deposition and nutrient availability is less spatially heterogeneous in stagnant water, which reduces the need for *N. lutea* to engineer the environment. Moreover, the mechanism for this engineering is lacking as there is little to no water movement that can be slowed (apart from occasional wind wave induced currents, but these are expected to be of minor importance in the small oxbow lakes that we had investigated). Hence, there is no benefit for *N. lutea* of investing in a large total submerged leaf area in stagnant water.

We showed that light intensity underneath a floating canopy is close to zero, making photosynthetic benefit from a submerged biomass only relevant in early spring when the floating canopy has not yet developed. Other evidence also points towards the negligible role of submerged biomass for photosynthetic purposes in summer. The photosynthetic efficiency of submerged leaves under saturating irradiance is only 5% of that of the floating leaves, and it is saturated at lower irradiance levels (200 and 2000 µmol m^{-2} s^{-1} respectively), making floating leaves by far the main photosynthetic tissue of *Nuphar lutea* (Snir *et al.*, 2006). Submerged leaves of *N. lutea* are only able to use carbon dioxide (CO_2) as water-dissolved inorganic carbon source (Snir *et al.*, 2006). The main supply of CO_2 comes from decomposition of organic material, respiration and liberation from sediment. Increased organic matter deposition will possibly enhance the available carbon concentration, but it still remains suboptimal compared to the floating biomass that has access to atmospheric CO_2 (Snir *et al.*, 2006, and references cited therein). Moreover, submerged leaves have a minimal number of undifferentiated cell layers, lacking a cuticle and having their stomata degenerated and functionless (Maberly and Spence, 1989).

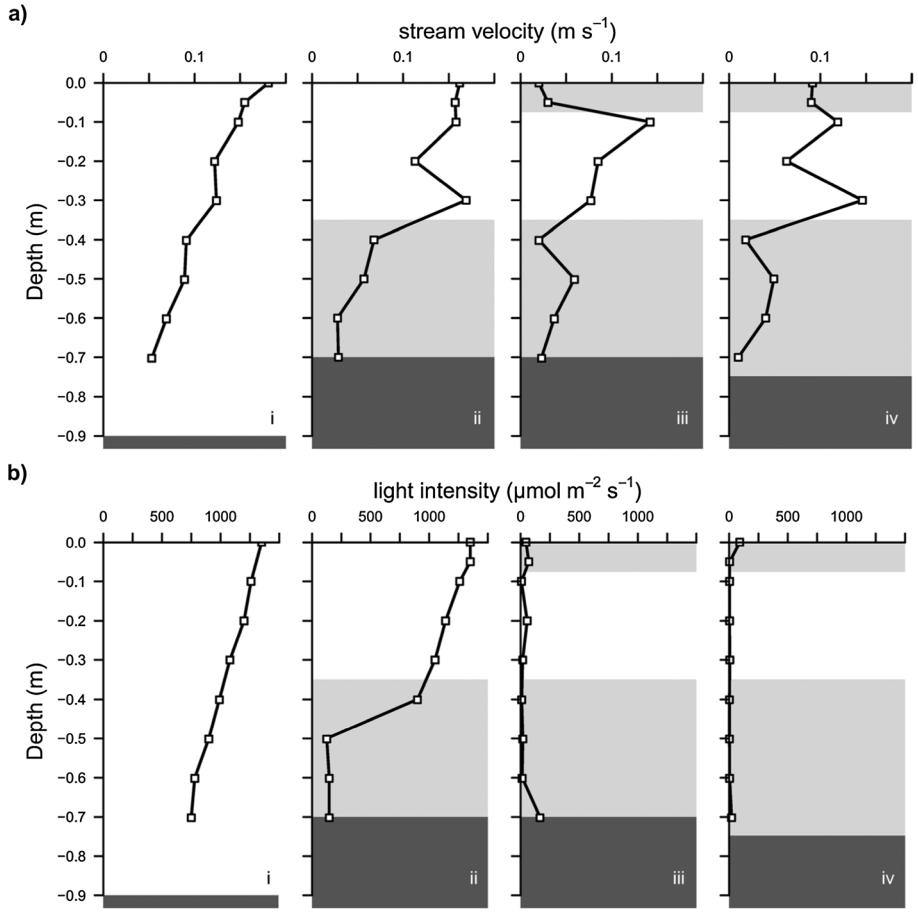

Figure 5. Velocity and light climate were measured on profiles through a *Nuphar lutea* patch in the Sidra River, near the village of Harasimowicze (site 1 in Figure 3). (a) Stream velocity profiles and (b) light intensity profiles in the river on a non-vegetated location (first profile (i), located 3 m upstream of the patch) and through a *Nuphar lutea* patch (profiles (ii) to (iv) in the upstream, middlestream, and downstream part of the patch). Total water depth differed per profile (dark gray background). The light gray background indicates the presence of leaf biomass: floating leaves in the top layer and submerged leaves near the bottom. Standard deviations were not recorded. EMF velocity measurements typically have an error of about 10%. Light measurements have an error smaller than 5%.

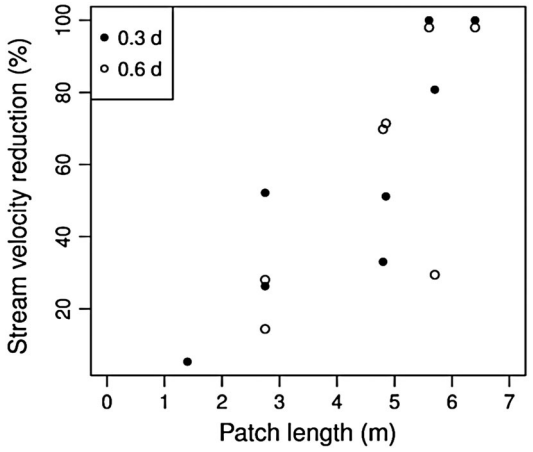

Figure 6. Relation between patch length of the submerged biomass (in meters) and flow velocity deceleration efficiency which is based on the relative difference between the patch upstream and downstream stream velocity (%). Stream velocities are measured on one-third (0.3*d*) and two-thirds (0.6*d*) of the submerged canopy height (measured from the stream bed). Relation is significant: Spearman rank test, $R^2 = 0.70$; $p < 0.001$; $n = 16$). Note that the patch length measurements have an inherent uncertainty of a few decimeters because of the continuous movement of the plants with the current.

Based on these field measurements, we have strong indications that patches of *Nuphar lutea* can be considered as ecosystem engineers. It depends on size (patch length) and density (total submerged leaf area) of the patch and is induced by habitat variation (presence or absence of a strong water flow). We can therefore accept hypothesis 1. We acknowledge that we did not take into account the 'causality effect': what if *N. lutea* seedlings in flowing waters preferentially establish in regions of the bed with finer sediment composition and higher nutrient content? This issue can only be tackled with an experimental approach which was beyond the scope of our field observations. However, this alternative is implausible because (i) vegetative propagation by extension of the rhizome system is the most important dispersal mechanism, and (ii) if the sediment is very loose and easily resuspended in water the seeds sink into the sediment to a depth from which seedling emergence is not possible (Barrat-Segretain, 1996).

Despite the potential contribution to early season photosynthesis, during the majority of the growing season, the submerged leaves of *Nuphar lutea* in rivers are shaded by the floating leaves. They therefore only contribute very limited to the total photosynthesis of the plant, leading to the acceptance of hypothesis 2.

It is also unlikely that the observed differences are caused by genetic differences between the individuals in oxbow lakes and rivers. Reproduction in *Nuphar lutea* is mostly vegetative and yearly winter flooding causes abundant exchange of seeds, plant fragments, or parts of rhizomes between the river and the oxbow lakes (Brock *et al.*, 1987), and individuals in both environments likely derive from the same gene pool. The

amount of flowers and flower bearing stems was also similar in both habitats implying an equal reproductive success (at least potentially since fertility measurements were not performed). Further, no differences in stem and petiole diameters were found, also consistent with an equal development of these organs. The difference in stem and petiole lengths in the different habitats (not significant for floating leaf petioles) probably reflects the difference in water depth on the different sampling sites (Brock *et al.*, 1987; Paillisson and Marion, 2006).

The ecological engineering capacity of the submerged leaves could also impact the geomorphology of the river. Submerged leaves of *Nuphar lutea* in lowland rivers such as the Biebrza decelerate the stream flow inside vegetation patches. We showed that this could be linked to an accumulation of smaller sediment particles inside patches, which is in accordance with other studies (e.g. Sand-Jensen, 1998; Cotton *et al.*, 2006). Since stream velocity is related to bed shear stress (the driving force for sediment transport), and sediment texture is a measure for shear strength of the sediment bed (the resisting force against sediment transport), it could be expected that the patches will have an effect on the sedimentation and erosion patterns, and hence on the geomorphologic changes of the river bed. The river bed was indeed 15 to 20 cm more elevated on profiles inside the patch near Harasimowicze compared to the profile upstream of the patch. These values are of the same order as found in other studies. Sand-Jensen (1998) and Schoelynck *et al.* (2012) for instance showed a 5 to 15 cm difference in mean elevation of the sediment surface between vegetated and non-vegetated zones in submerged macrophyte dominated lowland rivers. Although vegetative propagation of *N. lutea* is a slow process (Barrat-Segretain, 1996), its rhizomes can remain in the same location for many decades (even more than a century in cultivation; [Heslop-Harrison, 1955]), producing new shoots each year. A systematic and long-term influence of vegetation is therefore expected on local stream flow magnitude and direction, both laterally and longitudinally, which will induce local bathymetric changes.

Conclusion

Nuphar lutea had a significantly higher total submerged leaf area in running river water than in oxbow lake water. In running water, the benefit of having submerged biomass can be high, as this reduces the flow velocity, which likely increases the deposition of organic matter and improves nutrient availability relative to non-vegetated parts of the river bed. In oxbow lake water, where submerged biomass would not result in similar beneficial habitat modification, such dense and costly submerged biomass was absent. Our field measurements strongly support the hypothesis that submerged leaves in rivers engineer the environment: they trap organic matter and particulate nutrients and create oxbow lake-like conditions even in a river with relatively high stream velocities. In the long term this could have an impact on the local bathymetry (through sedimentation processes) and on local nutrient dynamics (through organic matter accumulation).

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